Unit–IV

Q. 15. ***Define flower and give an account of floral anatomy.***

Ans. The large majority of botanists, regard the flower as a modified sho and its parts homologous of leaves. Anatomically, the flower is a determina stem with crowded appendages, with internodes much shortened or obliterate The appendages are of leaf rank but differ from those of the vegetative stem function and shape. In the present text the flower is treated on the basis of th concept of homology between the flower and the shoot in their phylogeny an ontogeny.

Parts of the Flower and Their Arrangement

The flower consists of an axis, also known as receptacle and later appendages. The appendages are known as floral parts or floral organs. The are sterile and reproductive. The sepals and petals which constitute the caly and corolla respectively are the sterile parts. The stamens and the carpels a the reproductive parts. The stamens compose the androecium, whereas th free or united carpels compose the gynoecium.

The vegetative shoot shows unlimited growth, whereas the flower show the limited growth. In flower, the apical meristem ceases to be active after th formation of floral parts. In more specialized flowers there is a shorter growt period and they produce a small and more definite number of floral parts tha the more primitive flowers. In still more advance flowers there are specialize characters, such as, whorled arrangement of parts instead of spiral, adnation o parts of two or more different whorls, cohesion of parts within a whor zygomorphic instead of actinomorphic condition, and epigynous conditio instead of hypogynous condition.

Sepals : The sepals resemble leaves in their anatomy. Each sepal consist of ground parenchyma, a branched vascular system and an epidermis. Th chloroplasts are found in the green sepals but usually there is no differentiatio in the palisade and spongy parenchyma. They may contain crystal—containin cells, laticifers, tannin cells and other idioblasts. The epidermis of sepals ma possess stomata and trichomes.

The traces are similar in origin and number. From the evidence o vascular system, sepals are clearly, in nearly every case morphologically

bracts—that is, they have been derived directly from leaves and are not sterile sporophylls.

Petals : The petals also resemble leaves in their internal structure. They contain ground parenchyma, a more or less branched vascular system, and an epidermis. They may also contain crystal containing cells, tannin cells, laticifers and certain other idioblasts. They contain pigments—containing chromoplasts. Very often, the epidermal cells of the petals contain voltile oils which emit the characteristic fragrance of the flowers. In certain flowers the anticlinal epidermal walls of the petals are wavy or internally ridged, whereas the outer walls may be convex or papillate. The epidermis may also possess stomata and trichomes.

Stamen : Commonly the stamen consists of a two-lobed four-loculed anther. The anther is found to be situated on a slender filament which bears single vascular bundle. In certain primitive dicotyledonous families the stamens are leaf-like and possess three veins, whereas in advance types they are single-veined.

The structure of filament is simple. The vascular bundle is amphicribral and remains surrounded by parenchyma. The epidermis is cutinized and bears trichomes. The stomata may also be present on the epidermis of both anther and filament. The vascular bundle is found throughout the filament and culminates blindly in the connective tissue situated in between the two anther-lobes.

The outermost wall of the anther is the epidermis. Just beneath the epidermis there is endothecium which usually possesses strips or ridges of secondary wall material mainly on those walls which do not remain in contact with the epidermis. The innermost layer is composed of multinucleate cells, this is nutritive in function and known astapetum. The wall layers which are located in between the endothecium and tapetum are often destroyed during the development of the pollen sacs. On the maturation of the pollen the tapetum disintegrates and the outer wall of the pollen sac now consists of only the epidermis and endothecium. At the time of dehiscence of the anthers the pollen are released out through stomium.

Gynoecium : The unit of gynoecium is called the carpel. A flower may possess one carpel or more than one. If two or more carpels are present they may be united or free from one another. When the carpels are united the gynoecium is known as syncarpous; when they are free the gynoecium is said

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to be apocarpous. A gynoecium with single carpel is also classified as apocarpous. The apocarpous gynoecium is termed simple pistil, whereas the syncarpous gynoecium is termed compound pistil. The carpel is commonly interpreted as foliar structure. The carpel of an apocarpous or syncarpous gynoecium is being differentiated into the ovary and the style. The upper part of the style is differentiated as a stigma. The stigma is sessile.

The ovary consists of the ovary wall, the locule or locules and in a multilocular ovary, the partitions. The ovules are found to be situated on the inner oradaxial (ventral) side of the ovary wall. The ovule-bearing region forms the placentae. According to Puri (1952) the position of the placentae is related to the method of union of carpels. In a carpel the placentae occurs close to the margin. Since there are two margins, the placentae is double in nature. The two halves may be united or separate. The number of double placentae in compound ovaries is equal to number of carpels. When the carpels are folded, the ovary is multilocular and the placentae occur in the centre of the ovary where the margins of the carpels meet. This is axile placentation. When the partitions of the ovary disappear, it becomes free-central placentation. When the carpels are joined margin to margin and the placentae are found to be situated on the ovary placentation is parietal.

Most commonly the carpels has three veins, one dorsal or median and two ventral or lateral, and the vascular supply of the ovules has been derived from the ventral bundles. The vascular bundles of the ovary, possessing axile placentation appear in the center of the ovary, with the phloem turned inward and the xylem wall, the outward.

The ovary and style are composed of epidermis, ground tissue of parenchyma, and vascular bundles. The outer epidermis is cuticularized and may have stomata. The ovule consists of a nuclellus which encircles the sporogenous tissue. There are two integuments of epidermal origin, and a stalk, funiculus. The ovule consists of parenchyma and contains a more or less dominant vascular system.

Vascular Anatomy

The study of the vascular anatomy has helped in solving many intricate problems of floral morphology. It has shown that many structures are not what they appear to be or what they are commonly taken to be. The fundamental vascular plan remains more or less unaltered and can always be of some help (Puri, 1952).

Morphologically the flower is a determined shoot with appendages, and these appendages are homologous with leaves. This commonly accepted view is sustained by the anatomy of the flowers. Flowers, in their vascular skeletons, differ in no essential way from leaf stems. They are often more complex than most stems. Taxonomy and comparative morphology have in large measure determined the structural nature of the flower. Anatomyof the flower has aided in the solution of certain puzzling conditions.

Pedicel : The pedicel and the receptacle have typical structure, with a normal vascular cylinder. The cylinder may be unbroken or it may contain a ring of vascular bundles. In the region where floral organs are borne, the pedicel expand into the receptacle. The vascular cylinder also expands and the vascular bundles increase somewhat in number, and finally traces begin to diverge.

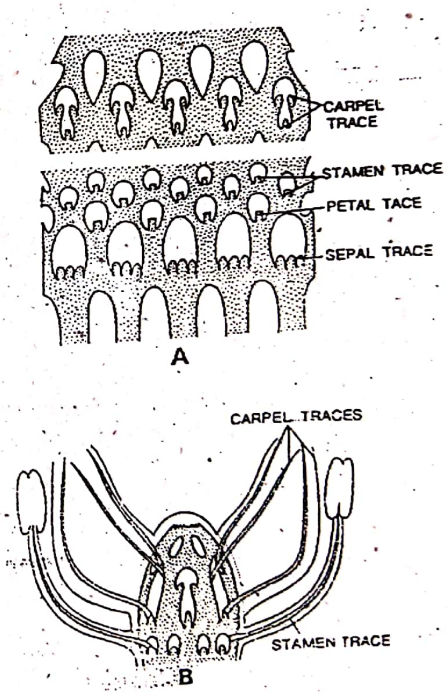

Fig. 15.1 Anatomy of the floral parts. A and B. diagrams showing vascular structure of Aquilegia.

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In the simplest cases vascular traces for different organs and whorls of organ arise quite independently (e.g., in Aquilegia). In other cases various degrees o fusion may take place between bundles situated more or less in the same sectors

The appendage traces are derived from the receptacular stele exactly a leaf traces are derived in typical stems. When the floral organs are numerou and closely placed, the gap of traces break the receptacular stele into meshwork.

Sepals : The sepals are with very few exceptions, anatomically like th leaves of the plant in question. A sepal usually receives three races derive from the same or different sources. As regards the morphological nature of th sepals, they have oftenbeen considered as equivalent to bracts and foliage leaves Such a view is born out by a study of vascular anatomy which reveals practically the same vascular pattern as exists in foliage leaves and bracts of the same plant.

Petals : In their vasculár supply the petals are sometimes leaf like, bu much more often they are like stamens. The petals may have one, three o several traces. Very commonly here is but one

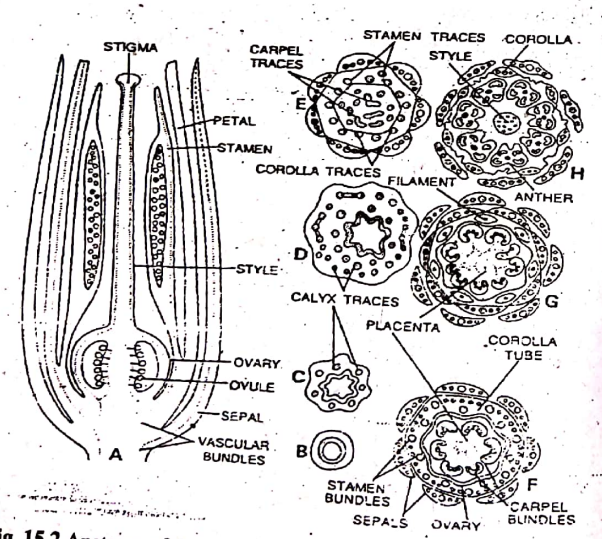

Fig. 15.2 Anatomy of the flower. A, L.S. of tomato flower; B, the pedicel shows a cylinderical vascular region encircling a pith and delimited on the

outside by the cortex; C—D, in the receptacle and level of attachment of the sepals, traces diverge into these appendages; D—E, the traces diverge into the corolla, one to each petal (in most dicotyledonous flowers); E—G, traces to the stamenss, typically one to each stamen; the carpellary supply of one, three, five or more traces to each carpel; H, a prolongation of the vascular supply into the style (After Esau).

trace. The petals appear to be sometimes modified leaves, like the sepals but in the great majority of families they are sterile stamens. However, since stamens are the homologous of the leaves, it is not always possible to determine from anatomical evidence along whether one trace petals in certain families are modified stamens or whether they have come more directly from leaf-like structures.

Stamens : A stamen generally receives a single trace which remains almost unbranched throughout its course in the filament. In the another region it may undergo some branching. In a few Ranalian families and rarely elsewhere as in some members of the Lauraceae and Musaceae, three traces are present in each stamen. In Ravenala (Musaceae) each filament is traversed by 25 to 28 small vascular bundles. Most of these disappear as the another is approached, and the system of central bundles consisting of three or four bundles, continues into the connective. From other evidence the above mentioned families appear to be fairly primitive, it seems highly probable that the single trace condition is one of reduction from three.

In the simple flower of Quilegia the stamen traces pass off, one to each organ in several whorls. Above the supermost whorl of stamens the vascular cylinder becomes complete again.

Carpels : The carpel is commonly looked upon as a leaf-like organ folded upward, i.e., ventrally with its margins more or less completely fused and bearing the ovules. This conception has been supported by the anatomy. The details of origin, number and course of the bundles forming the vascular supply are exactly like those of leaves the carpels has one, three, five or several traces. The three trace carpel is most common. The five-trace, carpel is nearly as common as the three traces, and carpels with seven, nine and more traces are increasingly less and less common. The evidence that the one-trace carpel (nearly always an achene) has been derived by reduction from the three-trace type. The median trace which leaves the stele below the other carpel traces, is known as the dorsal trace because it becomes the dorsal (midrib) bundle of the folded organ. The outermost traces are known as ventral or marginal traces because they become the bundles that run along the ventral edge of the carpel, i.e., along or

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near the margins of the organ of it were unfolded. The upward and inward folding of the sides of the carpel brings about the inversion of

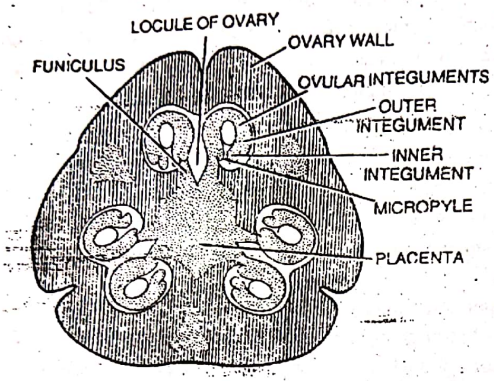

Fig. 15.3 The flower. T.S. of the ovary of Lilium, showing six anatropous ovules and the manner of placentation.

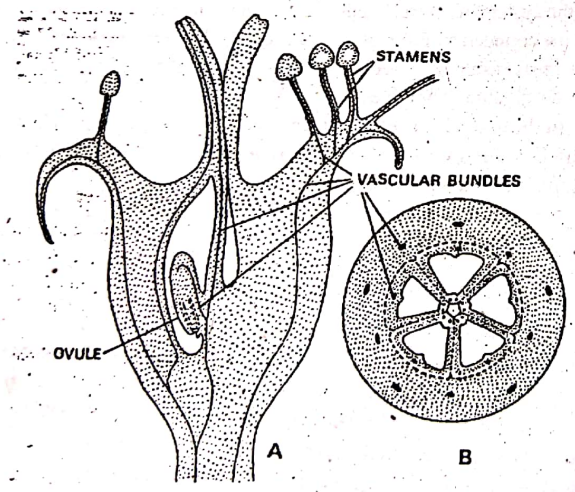

Fig. 15.4 The vascular system of the flower in Malus pumila. A, vertical section; B, transverse section.

these ventral bundles. The phloem remains on the ventral side in the carpel, whereas it is on the dorsal side in the midrib (dorsal) bundle. This important condition may be easily understood when it is remembered that the carpel is leaf-like, with its margins folded upward. The ovule traces are derived from the ventral bundles.

When floral parts are fused, the vascular bundles of these parts may also be fused. If carpels are united, the lateral bundles, either those of the same carpel or those of two adjacent carpel, may be fused in pairs. The fusion in the vascular tissue of a carpel may be present in the ventral bundles from an origin as one trace throughout their length, or may exist only in part of the carpel; where the ventral bundles arise as separate traces, they may unite at any point in their course.

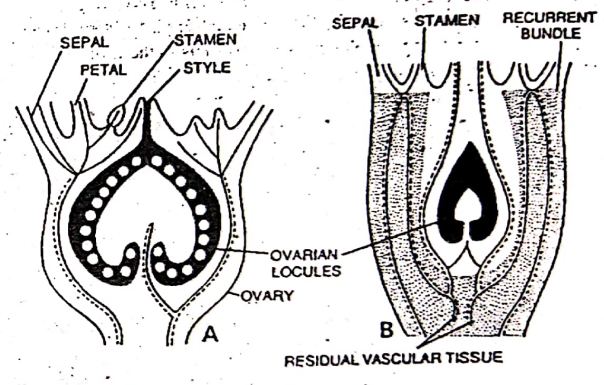

Fig. 15.5 Anatomy of the flower—the inferior ovary, The xylem is represented by solid lines ad phloem by broken lines. A, the ovary embedded within the floral tube (Samolus floribundus); B, In Darbya the ovary remains embedded in the invaginated receptacles (shown by dots). Here the receptacular nature of the outer tissue is indicated by the presence of recurrent bundles with inversely oriented xylem and phloem (After Douglas, 1944).

In syncarpy there are fusion changes similar to those in free carpels. The lines that separate the carpels and their margins have been disorganised. The inverted ventral bundles, form a ring of bundles in the centre. These bundles usually lie in pairs. Here each pair consists of the ventral bundles of the same

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carpel or more of ten of bundles from each of two adjacent carpels. In the centre of a three carpellary syncarpous ovary there may be a ring of six or three ventral bundles. If the ring consists of three bundles, each bundle is morphologically double and represents either the two ventral traces of one carpel or one from one carpel and one from the adjacent carpel.

Several workers proposed that the evolutionary changes in the structure of the gynoecium of the flower of angiosperms involve various manners of union of carpels of the same flower. In such angiospermous flower the carpel may become joined by their margins to the receptacle (fig. 15.6. B) or they may grow together laterally in a closed folded condition (Fig. 15.6.C), or they may become laterally united in an open folded condition (Fig. 15.6. A). The junction

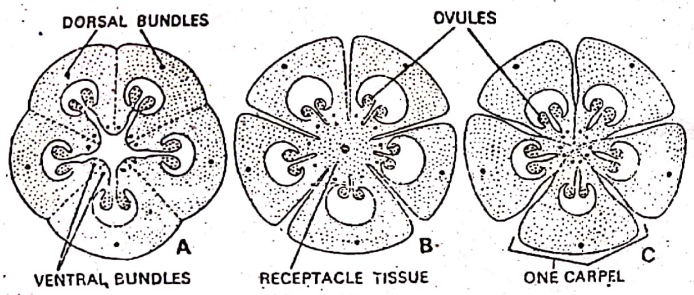

Fig. 15.6 The flower Gynoecia in transections showing syncarpous tendencies.

of carpels in an open condition may result in a unilocular ovary showing parietal placentation as shown in fig. 15.6 A. Folding combined with union of carpels with each other may form an ovary with as many locules as there are carpels. In such cases the ovules are borne on the central column of tissue where the carpels come together showing, axile placentation (Fig. 15.6 B, C).

The inferior ovary : The inferior ovary is formed by the adnation of the sepals, petals and stamens to the carpels or by the sinking of the gynoecium in a hollowed receptacle with fusion of the receptacle walls about the carpels.

Q. 16. ***Write an essay on nodal anatomy.***

Ans. **Nodal Anatomy**

Leaf Traces and Leaf Gaps : A shoot bears nodes and internodes. At each node, portions of the vascular system are deflected into the leaf, which is attached at this node. A vascular bundle located in the stem but directly related

to a leaf, to represent the flower part of the vascular supply of this leaf, is termed the leaf trace. The leaf trace is defined as follows—The leaf trace is a vascular bundle that connects the vascular system of the leaf with that of the stem. A leaf trace is extended between the base of a leaf and the point where it is completely merged with other parts of the vascular system in the stem. One or more leaf traces may be associated with each leaf.

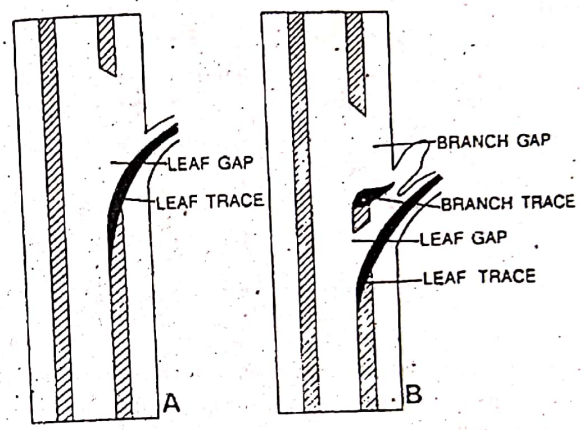

Fig. 16.1. Leaf and branch traces and gaps. A, L.S. of node through leaf trace and gap; B, L. S. of node through branch trace and gap.

In the shoot of a pteropsid (seed plants and ferns) where the leaf trace diverges into a leaf, it appears as though a portion of the vascular cylinder of the stem is deflected to one side. Immediately above the diverging trace, a parenchymatous tissue is being differentiated instead of vascular tissue in the vascular region of the stem for a limited distance. The parenchymatous regions in the vascular system of the stem, located adaxially from the diverging leaf traces, are called leaf gaps or lacunae. Actually these gaps are not breaks in the continuity of the vascular system of the axis. Lateral connections occur between the tissues above and below the gap. In transverse sections of an axis at the level of a leaf gap, the gap resembles an interfascicular area.

The gaps are quite conspicuous in the ferns and angiosperms where the vascular system in the internodal parts of the stem forms a more or less continuous cylinder. In some ferns the leaves are so crowded that the gaps formed at the successive nodes overlap one another and the vascular cylinder

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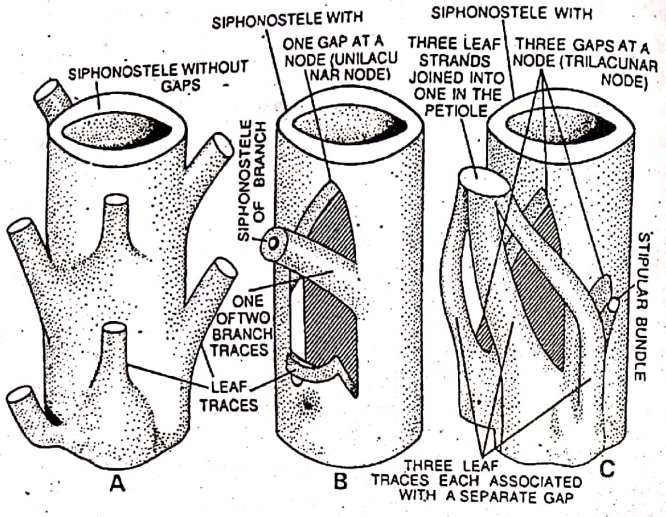
SIPHONOSTELE WITHOUT GAPS
SIPHONOSTELE WITH ONE GAP AT A NODE (UNILACUNAR NODE)
SIPHONOSTELE WITH THREE LEAF STRANDS JOINED INTO ONE IN THE PETIOLE
THREE GAPS AT A NODE (TRILACUNAR NODE)
SIPHONOSTELE OF BRANCH
STIPULAR BUNDLE
ONE OF TWO BRANCH TRACES
LEAF TRACES
THREE LEAF TRACES EACH ASSOCIATED WITH A SEPARATE GAP
A
B
C

Fig. 16.2 Primary vascular system. A, Selaginella—three-dimensional view, siphonostelic type without leaf-gaps; B, Nicotiana—unilacunar node, siphonostelic with leaf gap; C, Salix—trilacunar node, siphonostelic type with leaf gaps. (After Esau).

appears highly dissected. The transverse sections of such stems show a circle of vascular bundles with the parenchymatous leaf gaps. In certain ferns, gymnosperms and most angiosperms the vascular system consists of anastomosing strands. In such cases, the parenchyma that occurs above the diverging leaf trace becomes confluent with the interfascicular areas, thus the recognition of the gaps become uncertain.

There are three common types of nodes in the dicotyledons. The node with a single gap and a single trace to a leaf is known as unilacunar; the node with three gaps and three traces to a leaf (one median and two lateral) is known as trilacunar; and the node with several to many gaps and traces to a leaf is known as multilacunar. The most accepted concept is that the trilacunar condition is primitive in the dicotyledons and that the unilacunar and the multilacunar have been derived from it. Several monocotyledonous plants possess leaves with sheathing bases and nodes with a large number of leaf traces separately inserted around the stem. In ferns the number of traces to a

leaf varies from one to many, but they are always associated with a single gap. In gymnosperms a unilacunar node is common.

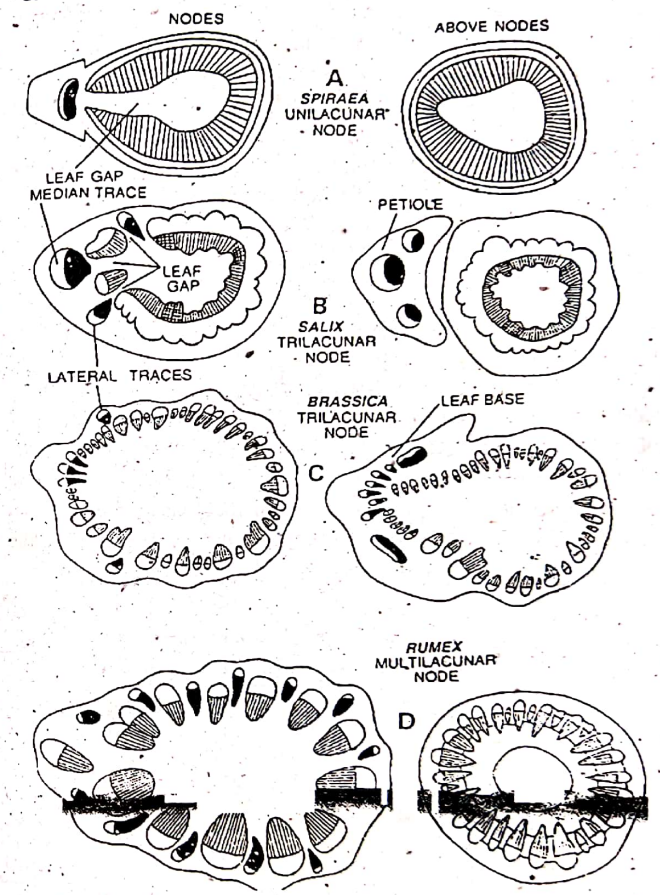

Fig. 16.3 Nodal anatomy of dicotyledons: A. Spiraea—each leaf has one leaf trace and one leaf gap (uilacunar node); B Salix—each leaf has three leaf traces and three leaf gaps (trilacunar node); C, Brassica—three leaf traces and three gaps per leaf (trilacunar node); D, Rumex—many leaf traces and many leaf gaps per leaf (multilacunar node).

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The leaf trace relationships at the nodes are thought to be of phylogenetic importance, and therefore, nodal anatomy is concerned with the study of systematics and phylogeny of angiosperms.

Nodal Anatomy in Wheat (Monocot) Stem :

In the wheat stem the course of the vascular bundles through the internode and the leaf sheath is almost parallel. Near the node the leaf sheath is considerably thick and attains its maximum thickness just above its union with the stem. On the other hand, the stem has the smallest diameter above the junction with the leaf seath. The stem is hollow in the internode and solid at the node. The sheath remains open on one side at higher levels, just near the node. Massive collenchymatous bundle caps are present in the bundles of leaf sheath.

Just beneath the junction of the leaf sheath and stem and smaller of the leaf traces are prolonged in the peripheral part of the axis, and the larger leaf traces become part of the inner cylinder of strands. The internodal bundles located above the leaf insertion assume, just above the node a horizontal and oblique course, and are reoriented toward a more peripheral position in the node and below it. These horizontal and oblique bundles variously branch and coalesce, and their number reduces. The large leaf traces and the bundles from the internode above the insertion of the leaf make the inner cyllinder of the bundles of the next lover internode.

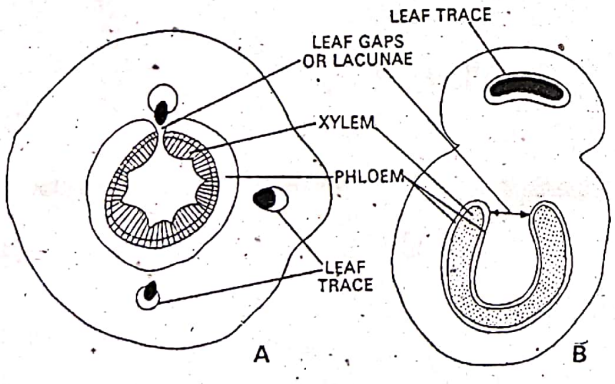

Fig. 16.4 Nodal anatomy. A, nodal anatomy of Picea (a conifer) in transection; B. nodal anatomy of adiantum (a fern).

Q. 17. ***Discuss the role of root apical meristem in the primary organisation of root.***

Ans. During the later stages of development of embryo, the cells at the root pole become arranged in a pattern characteristic of the species. This group of cells comprises the apical meristem of the primary root. The cells of this region are all relatively undifferentiated and meristematic, densely protoplasmic and with large nuclei and they all undergo active division. The tissues of the mature root are eventually derived from a number of these cells of the apical meristem, which are termed initials. In contrast to the apical meristem of the shoot, that of the root produces cells not only toward the axis but also away from it, for it initiates the root cap and because of the presence of root cap the root meristem is not terminal but subterminal in its position, in the sense that

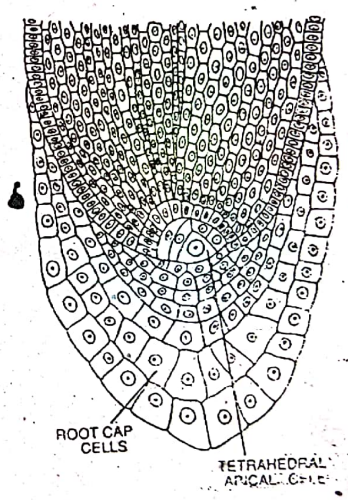

Fig. 17.1. Root apex of Pteris (fern) in longitudinal section showing tetrahedral apical cell.

it is located beneath the root cap. The root apex also differs from the shoot meristem in that it forms no lateral appendages comparable to the leaves, and no branches. The root branche are usually initiated beyond the region of most active growth, and they arise endogenously. It also produces no nodes, and internodes, and therefore, the root grows more uniformly in length than the shoot, in which the internodes elongate much more than the nodes.

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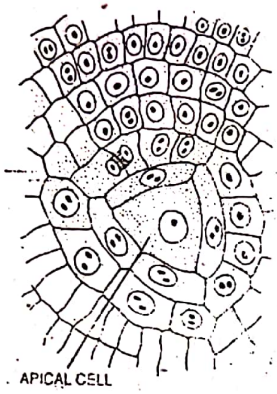

Fig. 17.2. Root apex of Pteris (fern) in cross section showing foursided apical cell, one side being in contact with the root cap.

Apical Cell Theory :

This theory was put forth by Nageli. In the roots of vascular cryptogams (pteridophytes), e.g., Drypteris, a single tetrahedral apical cell is present, it is generally thought that by its division this gives rise to all the tissues of the root. However, the apical cell theory was superceded by the histogen theory.

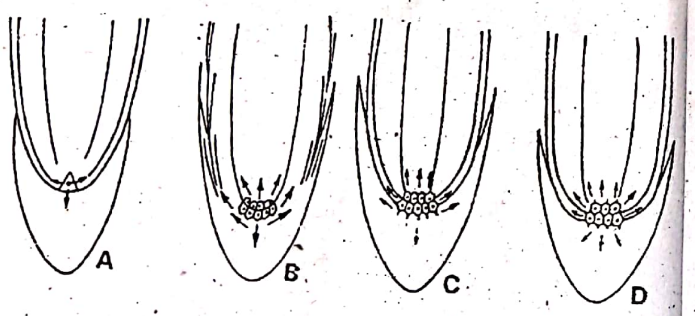

Fig. 17.3. The root apex. Diagrams showing different root apex types, A, initial solitary, cap distinct; B, initials in two groups, cap not distinct structurally; C, initials in three groups, cap not distinct; D, initials in three groups, cap distinct, and independent in origin. (After E. & M.)

In number, the initials range from one to many. Where the initials are more than one, they are arranged in one to four fairly distinct, uniseriate groups. In each group there are one to several initials. Where there is more than one

group, the groups lie adjacent to one another on the longitudinal axis of the root. Each of these groups quickly develops one or more growth zones. In many plants these zones appears to represent 'the histogens'. The terms

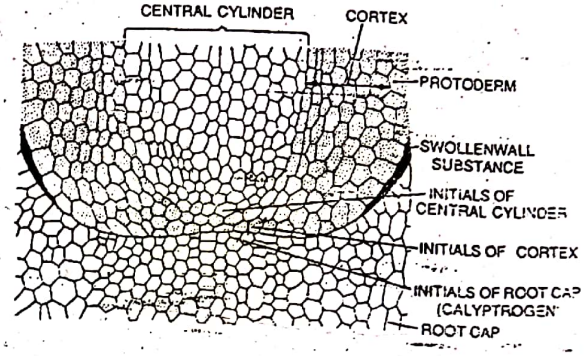

Fig. 17.4. The root apex. Root tip of Zea mays in L. S. The swollen wall substance originates through the gelatinization of the wall between the root cap and the protoderm.

dermatogen, periblem and plerome are no longer in general use in descriptions of stem ontogeny but they have been continues to indicate general zones in studies of root development. A fourth histogen, the calyptogen, in added where the cap has an independent origin. There are basic patterns for the major plant group. The pattern is determined by the number of initials, the number of groups of these intials, the zone formed by each group, the morphological nature of the cap, and the degree of independence of the cap.

The vascular cryptogams such as horsetails, most of the ferns, some species of Selagine have a solitary apical cell in the root. This one cells forms the entire root and the cap.

In many gymnosperms there are two groups of initials. The inner forms the plerome; the outer forms the periblem and the cap. The cap appears as a distal proliferation of the periblem. It dermatogen is not set off at the very apex, as in all other groups, but is formed from the layers the periblem a little away from the apex where the base of the cap is separated from the periblem.

In the angiosperms there are three, rarely four groups of initials. In the dicotyledons the disti group forms the cap and the dermatogen; the median group, the periblem; the innermost, that plerome. The most characteristic is

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the common origin of cap and dermatogen. In monocytyledons there are thre groups of initials which form four zones, but the outermost, independentl forms the cap, and that next beneath, the dermatogen and periblem. The mo characteristic of this type is that the origin and structure of cap is independen Moreover, the two zones that are formed by one group of initials (dermatoge and periblem) and different from those (cap dermatogen) similar formed in th dicotyledons.

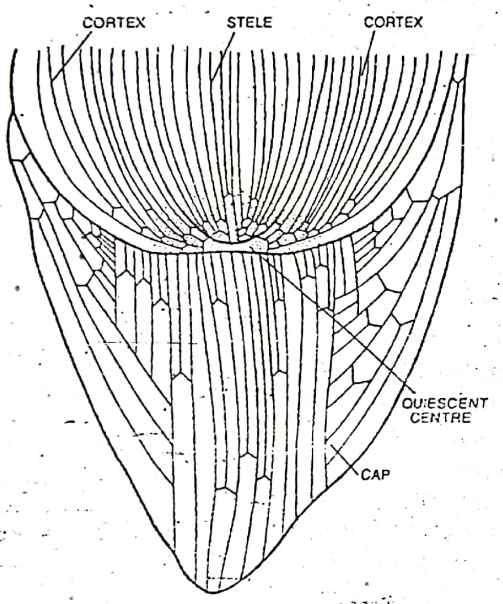

Fig. 17.5. Root apex. Pattern of cell lineages in the root apex of Zea mays. The cortex, vascular cylinder or stele, root cap and quiescent centre are indicated. (After Clowes).

.Körper-kappe theory :

This theory was put forth by Schuepp in 1917. Since the root changes i diameter during growth, there are various points at which a single longitudina file of cells has become a double file as a result of cell division. At these point a cell first divides transversely and there after one of its daughter cells divide longitudinally. This was known as T division, because the cell walls form A T

shaped structure. In some zones of the root, mainly in the centre, the bar of the T faces the root apex, in other it faces away from the apex (⊥). These zones of the root, delimited by the planes of cell division, were called Korper (body) and Kappe (cap) respectively. This theory may be compared with the tunica-corpus theory in the shoot apex.

Mainly in roots with a very regular arrangement of cells in the apical meristem, such as of Zea mays, it is possible to conclude from the study of cell lineages that there is a central region of cells which divide rarely or not at all. The cells on the periphery of this hemispherical or cup-shaped region are meristematic. This inactive or passive region of cells is known as 'quiescent centre'.

The Quiescent Centre :

In the apical meristem of root of Zea mays, and other plants with a regular arrangement of cells in the apical meristem, it is possible to conclude from the study of cell lineages that there is a central region of cells which divide, rarely or not at all. These inactive or passive cells constitute the quiescent centre. The cells on the periphery of this hemispherical or cupshaped region are meristematic and may be regarded as the constituents of the promeristem (Clowes, 1958). By various techniques, the existence of quiescent centre, has now been demonstrated in the root apices of a considerable number of species. The quiescent centre develops during the ontogeny of the root (Clowes, 1958). A quiescent centre is not found in the roots with a single apical cell. In 1956, Clowes was able to show that there was a central region (quiescent centre) in the roots of Zea where the cytoplasm had the lower content of RNA and where the cells had smaller nucleoli. He was also able to demonstrate that the cells in the quiescent centre did not actively synthesize DNA.

The physiological and cytological properties of the cells in the quiescent centre have now been studied in a number of species. The cells in the region have a lower concentration of DNA, RNA and protein than any other cells in the root apex (Clowes, 1958; Jensen, 1958). The cells of quiescent centre also have fewer mitochondria, little endoplasmic reticulum, and the smallest dictosomes, nuclei and nucleoli (Clowes, 1964). They are less sensitive to radiation damage than other cells of the meristem (Clawes, 1959, 1964).

The function of the quiescent centre may be to provide a reserve block of diploid cells within the root. The quiescent centre may be the site of hormone synthesis.

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The Promeristem :

Clowes (1961) has defined the promeristem as that part of the root apex which is capable of giving rise to all the tissues of the root. In the roots of vascular cryptogams, for example, the promeristem would consist of apical cell only, and in angiosperms it would comprise the initials of the histogens. This way there is a tendency to regard the promeristem as a rather small region, situated terminally in the root apical meristem, below the root cap. On the basis of modern work it has been suggested that in many roots the promeristem is broad and consists of a somewhat cupshaped group of cells on the periphery of a central inactive region. This grouping of the initial cells of the promeristem was suggested by Clowes (1950) on the basis of an anatomical study of the root apex of Fagus sylvatica.

Theories of Structural Development and Differentiation

As has been discussed by several workers (Foster, 1939, 1941; Sifton, 1944; Wardlaw, 1945), the view regarding the number, the arrangement, and the activity of the initial cells and their derivatives in the apical meristems has undergone many changes since the shoot apex was first recognized by Wolff in 1759 as an undeveloped region from which the growth of the plant proceeded.

The Apical Cell Theory :

This theory was put forth by Nageli in 1958. Solitary apical cells occur in many of algae, bryophytes and vascular cryptogams (pteridophytes). The discovery of the apical cell in cryptogams led to the concept that such cell exist in phanerogams (seed plants) as well. The apical cell was interpreted as a constant structural and function unit of apical meristems governing the whole process of growth. However, this was confirmed by later researches that this theory may hold good for cryptogams but is not applicable to the phanerogams. Further researches have refuted the universal occurrence of apical cells and replaced it by a concept of independent origin of different parts of plant body. The apical cell theory was superceded by the histogen theory.

The Histogen Theory :

This was introduced in 1870 by Hanstein who considered that the promordial meristem was sharply separable into three distinct zones or histogens. According to this theory the apical meristen or small mass of cells which are all alike and are in a state of division. These meristematic cells constitute promeristem. The cells of the promeristem soon differentiate into three regions—dermatogen, periblem and plerome. Every zone consists of a

group of initials and is called a histogen or a tissue builder. Dermatogen—This is the single outermost layer of the cells which later gives rise to the epidermis of the stem. In the root it is also single layered, but at the apex it merges into the periblem and just outside the periblem the dermatogen cuts off many new cells resulting into a small celled tissue, the calyptrogen, which

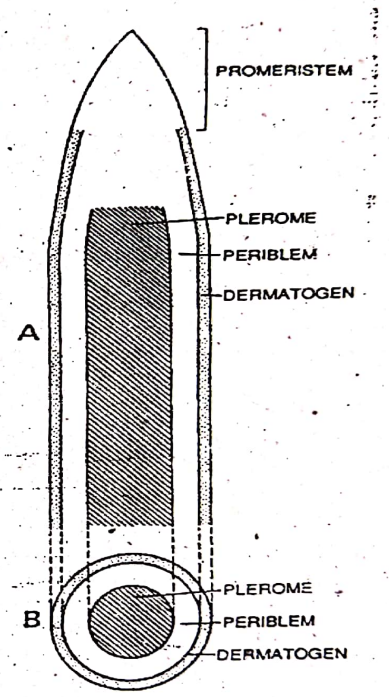

Fig. 17.6. The shoot apex—diagram showing histogen regions. A, longitudinal section; B, transverse section. (After E. & M.)

is also meristematic and gives rise to the root cap. Periblem—This region is found internal to the dermatogen, and is the middle region of the apical meristem. It is single layered at the apex but in central part it becomes multilayered. It develops into the cortex of the stem. In the roots it is also single layered at the apex and many layered in the central portion. In the case of root, it also develops into the cortex. Plerome—It is the central meristematic region of stem apex

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and lies internal to the periblem. It is also composed of thin walled isodiametri cells. Ultimately it develops and differentiates into the central stele consistin of primary vascular tissues and ground tissues, such as, pericycle, medullar rays, and medulla. In the roots the function of plerome is practically same as i stem. At a little distance behind the apex certain strands of cells show a tendenc to elongate. These strands of elongated cells make the procambium. Th procambial strands ultimately become differentiated, into vascular bundles. portion, however, remains undifferentiated, and it forms the cambium of th vascular bundle.

Recent investigations have revealed that there is no strict relationshi between the development of the histogens and various regions of plant bod and the segmentation and layering of the cells in the apical meristem. Howeve the distinction of these histogens in an apex cannot be made in some plants and in others the regions have no morphological significance.

The Tunica-Corpus Theory :

This theory was put forth by Schmidt in 1924. The apical cell theory an the histogen theory were developed with reference to both the root apex and

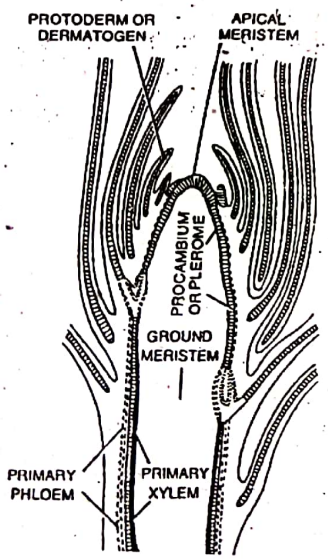

Fig. 17.7. Apical meristems. L. S. of stem tip (diagrammatic) showing the histogens.

the shoot apex. Later attention became centred largely on shoot apices, and with the result the tunica corpus theory was developed. Accroding to this theory, there are two zones of tissues in the apical meristems—the unica consisting of one or more peripheral layers of cells, and the corpus, a mass of cells enclosed by the tunica. According to this theory different rates and method or growth in the apex set apart two regions. The layers of the tunica show predominantly anticlinal divisions, that is, they are undergoing surface growth. In the corpus the cells are large, with arrangement and planes of cell division irregular, and the whole mass grows in volume. Each layer of the tunica arises

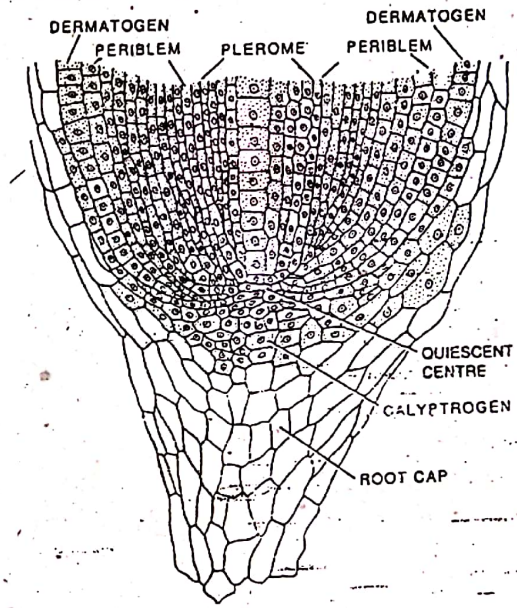

Fig. 17.8. Root apex. L. S. of a tip of onion root showing histogens and root cap.

from a group of separate initials, and the corpus has one layer of such initials. In the tunica the number of layers of initials in equal to the number of layers of tunica, that is, each layer of tunica has its own layer of initials. The corpus arises from a single tier of initials which divide first periclinally to give is to group of derivatives, which divide in various planes resulting in the formation of the inner mass of cells.

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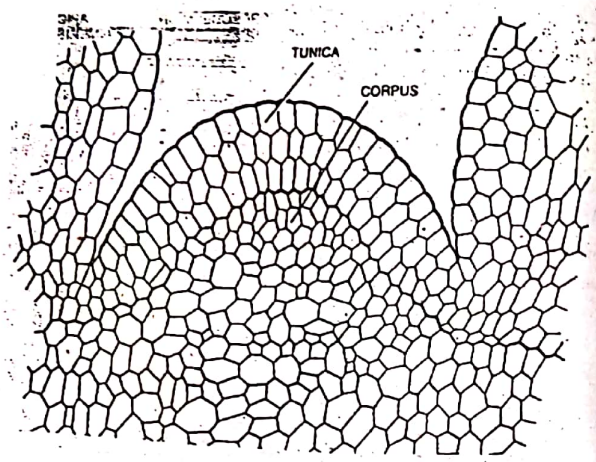

Fig. 17.9. Apical meristem. L. S. through shoot apex of Vinca; showing three-layered tunica and corpus beneath it.

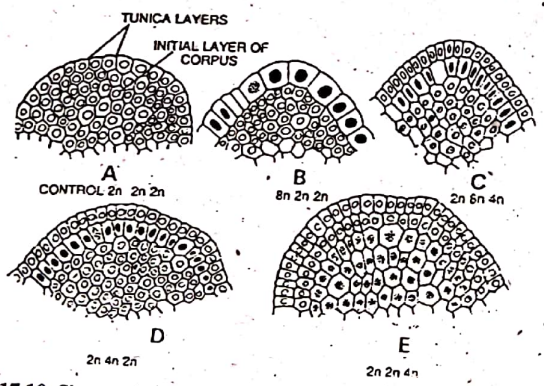

Fig. 17.10. Shoot apices of Datura. A, diploid plant; B—C, periclinal cytochimeras. The chromoson combinations in the various apices are indicated by the values given below else diagrams. The first figure of each group (i.e., 2n, 8n, 2n and 2n) of three refers to the five tunica layer; the second (i.e., 2n, 2n, 8n, 4n and 2n) to second tunica layer; the third (i.e., 2n, 2n, n, 2n and 4n) to the initial layer of the corpus. The 8n cells are largest the 4n of are somewhat smaller, the 2n cells are smallest. In the tunica layer the divisions anticlinal, in the corpus they occur in various planes. (After Satina et. al., 1940).

The number of initials varies from few to many. For example, in small very slender apices, such as those of grass seedlings, there may be only one or two in the tunica and about two in the corpus.

In vascular plants, the differentiation of the zones of stem-apex follows more or less definite patterns that seem to be characteristic of the major groups. These patterns show increasing complexity from the lower to the higher groups and appear to represent a series in specialization from simplicity to complexity.

As regards the concept of tunica and corpus, there may be several types which are found in the stem apices of several vascular plants. The types may be as follows.

The primitive type of stem apex having no distinction of tunica and corpus : Lycopodium, Isoetes, Selaginella (pteridophytes) and cycads(gymnosperms) belong to this group. They have simple apices with surface initials and no distinction of tunica and corpus. In Lycopodium, the initiating layer is weakly defined, having uniseriate surface area which divides freely both anticlinally and periclinally. Here all the cells of the layer are morphologically alike. The anticlinal divisions increase the area of the surface layer, whereas the periclinal divisions formthe inner core.

The stem apices with weak tunica-corpus demarcation : The demarcation of tunica and corpus layers begins in some of the lower conifers. In Abies and Pinus (Coniferales), the initials make an apical uniseriate group. These initials further give rise to a central core and an enveloping uniseriate layer by both periclinal and anticlinal divisions. The uniseriate layer that envelops the central core suggests a tunica in appearance, but there is no clearcut demarcation between the tissues of two regions. However, in the apices of Sequoia sempervirens, the initials are a small group of surface cells in one tier, with both anticlinal and periclinal divisions. These divisions result in the formation of a dermatogen like layer and a central mass. The outer layer suggests a tunica and the central mass, the corpus. The species of Cryptomeria and Taxodium (Coniferales) have a fermatogen, in which there are no periclinal divisions. There appears to be structural segregation of tunica and corpus in the apices of many Coniferales, but there is only one tier of initials and no independent meristematic regions are recognized.

The stem apices with distinct tunica and corpus : In angiosperms the demarcation of meristematic zones of apical region is usually more distinct

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and definite than in lower groups. There the two sets of initials, one above the other, which give rise to tunica and corpus which seem to be completely independent. The tunica has no or only rare periclinal divisions. It ranges in thickness from one to several layers. Usually there occurs two or three layers. The larger numbers of tunica layers occur more frequently in the dicotyledons. A single-layered tunica occurs in the grasses. However, in monocotyledons the number of tunica layers is one to three. In Zea, tunica divides periclinally, which shows an exceptional condition. The number of the layers in tunica may vary even in an individual plant. The corpus varies from a large complex type to a slender, simple type.

Significance of the tunica corpus theory : The tunica-corpus theory served well in the establishment of meristematic patterns of the shoot apices of seed plants. The position, number and behaviour of the initiating cells in seed-plant stems, and early stages in the development of primary body of the shoot are now much better understood. The tunica-corpus theory is of topographical value in studies of detailed development. The lateral organs of the stem, i.e., leaves, branches and floral organs, arise near the apex and studies of tunica and corpus have added greatly to a knowledge of origin and early development of these organs.

Q. 18. ***Describe ontogeny, structure and types of stomata.***

Ans. The Stoma : The opening in the epidermis through which gaseous interchange takes place between the intercellular spaces of the subepidermal cells and the atmosphere are known as stomata. These openings are spaces between two specialized epidermal cells which are known as guard cells, because changes in size and shape of these cells determine the opening and closing of the stoma (Fig. 18.1), Ordinarily, these two cells alone of the epidermal cells adjacent to the stoma differ from typical epidermal cells. Where other cells also are modified because of the presence of the stoma, and contribute in some way to the functional activity of the guard cells, such cells are known as accessory cells. This type of cell is restricted almost wholly to xerophytic plants. The term stoma is also, and perhaps preferably, applied to the opening in the epidermis plus the surrounding guard and accessory cells. In this usage the orifice is known as the stomatal opening or stomatal aperture.

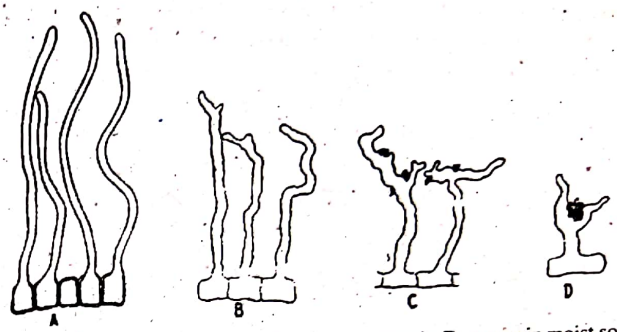

Fig. 18:1 Root hairs. A. grown in water or moist air; B, grown in moist soil : C. D. grown in dry soil. (Particles of soil adhere in C and D.) (After Schwarz).

Structure and Action of the Guard Cells : In all stomata the opening and closing is dependent upon changes in the turgor of the guard cells, increased turgor causing the stoma to open. The way in which the guard cells operate varies in different species with the shape of the guard cells and the thickening of parts of the wall. In a common type the walls of the guard cells are uniformly thickened and the guard cells are elliptical as seen in transverse section (Fig. 18.2F). With an increase in turgor these cells tend to become round in cross section, thus separating the closing walls of the stoma. In other tyeps that open in a similar manner, the wall is unevenly thickened (Fig. 18.2E). A modification of this same principle of change in the shape of a cell that is asymmetrical in cross section is found also in other types of stomata in which the walls are unevenly thickened. In these types the cell wall may be very thick, except at two points or regions known as "hinges." The lumen of such cells is elliptical or oval as seen in cross section, and with an increase of turgor tends to become round, thus causing a stretching or flattening of the thin parts of the wall with consequent opening of the stoma (Fig. 18.2 B, G, the hinges being the median point on the side of the aperture and the entire opposite wall). In another common type the guard-cell walls next to the aperture are somewhat thicker than those on the opposite side (Fig. 18.2H). Increase in turgor in guard cells of this type causes the thinner walls to stretch, and this, in turn, causes the entire cell to become more sharply curved and the opening enlarged. In the grasses and some other plants the ends of the guard cells are thin-walled and

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enlarged, whereas the central parts next the aperture are thick-walled and rigid (Fig. 18.2 I, J, K). With increase in turgor, these bulbous ends of the guard cells become distended and press against each other, forcing the rigid centers to separate and the stoma to open. Decrease in the turgor of the guard cells always results in the closure of the stoma.

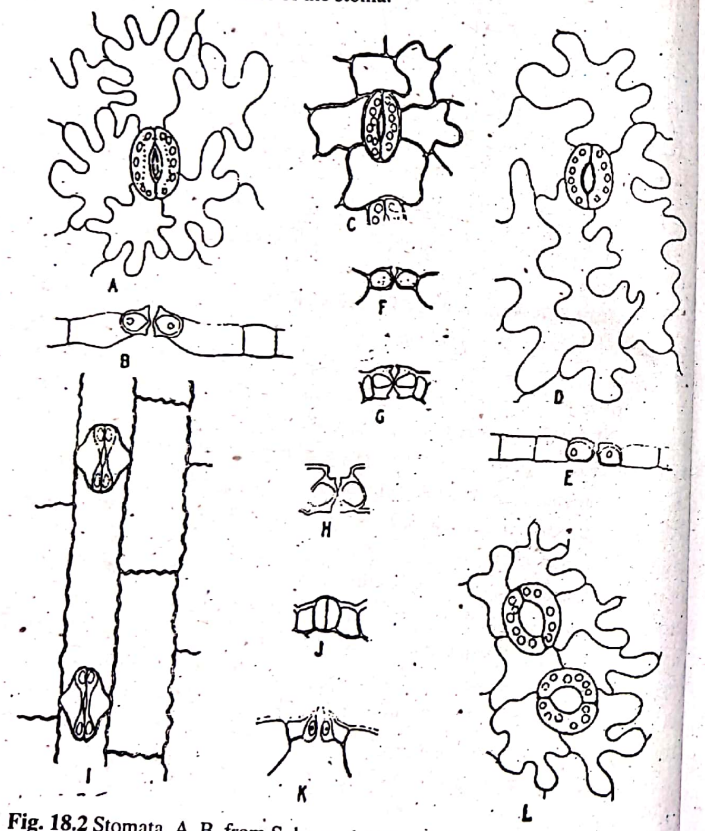

Fig. 18.2 Stomata. A, B, from Solanum luberosum, in face view and cross section; C, from Malus pumila; D, E, from Lactuca sativa; F, from Medeola virginica; G, from Aplectrum hyemale; H, from Polyganatum biflorum; I, J, K, from Zea mays; I, face view, J, cross section through end to stoma, K, median cross section; L, from Cucumis sativus. (F, G, H and J, after Copeland.)

The above statements are descriptive only of general stomatal structure. Other more or less distinct types exist, with variations in the shape of guard cells and position of the thickened areas of their walls. The details of structure about the opening vary greatly without different species, but area constant for some large groups, for example, the grasses and the gymnosperms. Differences in behaviour and fundamental form are not controlled by habitat, but marked modifications are found in xerophytes. The essential structural features are the same for all stomata.

The guard cells differ from other cells of the epidermis of which they are a part in that their protoplasts are more richly cytoplasmic, with a prominent nucleus, and chloroplasts and starch grains are usually present.

Functionally, stomata are of the greatest importance since it is through these openings that gaseous interchange between the intercellular space systems and the outer air takes place. Upon this diffusion through the stomata, the functions of respiration, transpiration, and photosynthesis largely depend.

Occurrence of Stomata : Stomata occur on all parts of the plant except the root. On floral organs and in aquatic plants they may be few, abortive, or lacking. They are most numerous on leaves except in those plants in which the leaves are reduced, and photosynthesis is in large measure restricted to the stems.

In leaves stomata may occur in both the upper and the lower epidermis; in woody plants they are commonly absent from the upper epidermis. The number per unit area tends to be greater in woody plants then in herbs, and greater in plants of dry and exposed, than of moist and sheltered habitats. It increases towards the apex and margin of the leaf where the cells decrease in size, the proportion of stomata to epidermal cells remaining the same. In woodland habitats the number per unit area increases with height above the ground. The number is apparently related to the humidity of the environment; variations in amount of light seem to have no effect.

Ontogeny of the Stoma : During the development of the epidermis a guard mother cell is formed by the division of one of the young epidermal cells. The guard mother cell divides to form the pair of guard cells. Accessory cells are derived from the same cell as the guard mother cell or from several adjacent cells.

Hairs : Appendages of the axis and leaves which consist only of epidermal cells are known as *hairs*, or trichomes. Such appendages are unicellular or

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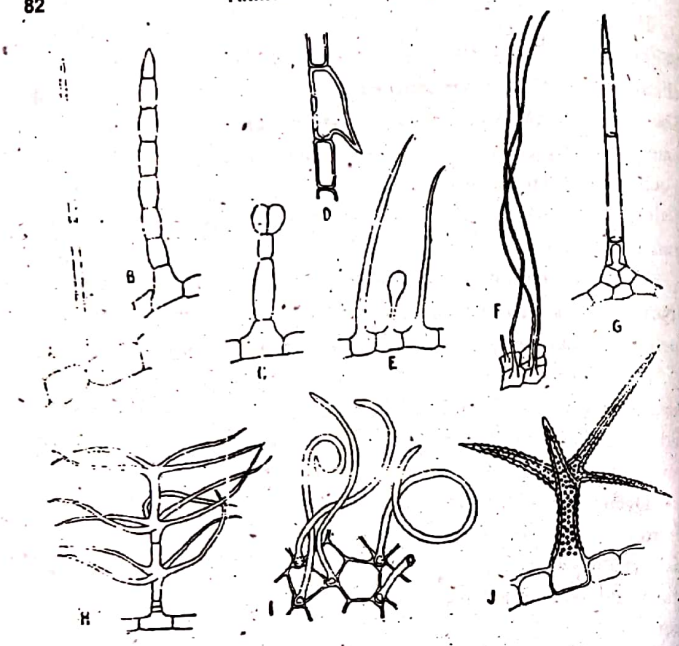

Fig. 18.3 Hairs. A, from corolla of Epigaea; B, from leaf of Coreopsis; C, from corolla of Phryma; D, from leaf of Avena; E, from calyx of Heliotropium; F, from stem of Onopordum; G, from leaf of Cucumis; H, from young leaf of Platanus; I, from fruit of Rubus strigosus; J, from stem of Aubrietia.

multicellular and occur in very many forms (Fig. 18.3). All transitional stages occur between the typical epidermal cell and one in which the outer wall is prolonged into a tube sufficiently pronounced to be considered a hair. Such intermediate cells, called papillose cells, are common upon petals and many leaves. So-called "unicellular" hairs are formed in two ways : by the prolongation of the outer wall of the epidermal mother cell, as in root hairs (Fig. 18.1); by the transverse division of the elongating mother cell—the outer daughter cell forming the hair, the inner a basal cell in the epidermis. Unicellular hairs assume numerous shapes, including elaborately forked and branched types (Fig. 18.3). Multicellular hairs likewise are found in innumerable types, and range from simple linear hairs of a few cells to complex, intricately branched,

or massive structures, involving considerable areas of the epidermis. Stinging hairs, scales, and many glandular hairs are complex multicellular structures. Root hairs are morphologically typical hairs.

The cells of hairs may be dead or living. If alive, the protoplasts contain little cytoplasm, unless the hair is associated with secretion of some type when the cytoplasm is abundant and richly granular. The thickness of the wall and its chemical nature vary greatly. Such hairs as those on the fruit of the peach and raspberry (Fig. 17.3), the flower of the willows, and the bud of the grape are very thick-walled. Cutinized and lignified hairs are frequent. Cotton "fibers" are cellulose hairs.

Hairs are connected with many functions, major and minor, but it is in the reduction of transpiration through the additional coating they provide that they are probably most important.

Q. 19. ***What is shoot apical meristem ? How does it play role in the primary organisation of shoot ? Give brief idea about the divergent view put forth in this regard.***

Ans. The apical meristem includes the meristematic initials and their immediate derivatives at the apex of a shoot or root. The apical meristem, thus delimited corresponds approximately to the promeristem, and to contrast with the partly developed derivatives of the promeristem, i.e., the protoderm, the ground meristem, and the procambium. This seems quite impracticable, to think of the apical meristem as consisting of the initiating cells only because cells may be poorly differentiated from their most recent derivatives.

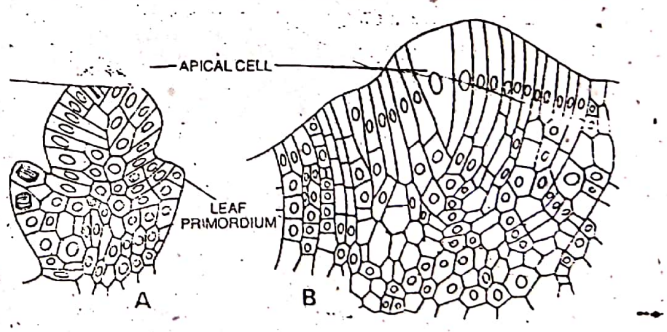

Fig. 19.1. Apical meristems. A, shoot apex with apical cell of Equisetum shoot; B, shoot apex of Pteridium.

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The terms shoot apex and root apex are more convenient to use instead of apical meristem of the shoot and apical meristem of the root, respectively. In the similar way, the terms shoot apex and root apex are more conveniently used as the substitutes of growing points. Growth in the sense of cell division, which is characteristics of the meristematic state, is not restricted to the so-called growing point but occurs abundantly—and may be even more intense—at some distance from the apical meristem (Wardlaw, 1945; Goodwin and Stepka, 1945). On the other hand, growth in the sense of increase in size of cells, tissues, and organs is most pronounced, not in the apical meristem, but in its derivatives.

Initials and Derivatives

An initial or initiating cell, is a cell that remains within the meristem indefinitely with the addition of cells to the plant body by combining self-perpetuation. The concept regarding meristematic initials, implies that a cell is an initial, not because of its inherent characteristics, but simply because of its particular position in the meristem, a position that cannot be treated as permanent.

The number of initials in root and shoot apices is variable. In most of pteridophytes a single initial-cell occurs at the apex. In the lower vascular plants, as well as in the higher, several initials are present. The single initial in its morphology is quite distinct from its derivatives and is commonly known as the apical cell. If the initials are numerous, they are called apical initials.

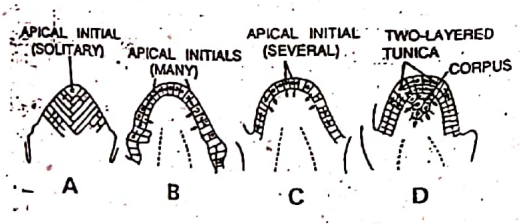

Fig. 19.2. Position and planes of division of stem-apex initials. A, initial solitary, with oblique and anticlinal divisions; B, initials many, superficial, divisions both anticlinal and periclinal; C, initials several, superficial, divisions both anticlinal and periclinal; D, initials in three tiers, the two outer, with anticlinal divisions, forming a two-layered tunica and the innermost, with divisions in all planes, forming a corpus. (After Eames and MacDaniels).

Usually the apical initials occur in one or more tiers. If there is only one tier, all cells of a plant body are ultimately derived from it. On the other hand, different parts of a plant body are derived from different groups of initials.

Vegetative Shoot Apex

The vegetative shoot apices vary in shape, size and cytohistologic structure, and in their relation to the lateral organs. The shoot apex of Pinus and other conifers are commonly narrow and conical in form. In Cycas (cycads) and Ginkgo they are usually broad and flat on the other hand the apical meristem of a grass and some other monocotyledons remains elevated above the youngest leaf primordium. In many dicotyledons the apical meristem rises above the promordia, and in other cases it appears to be sunken beneath them. The diameters of apices range from 90μ in some angiosperms to 3.5 mm in Cycas revoluta (Foster, 1949). The size and shape of the apex marked by change during the plant development.

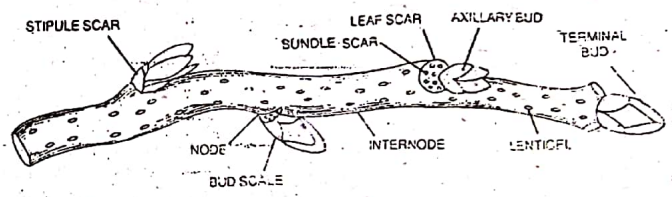

Fig. 19.3. Apical Meristem. Stem of Aesculus hippocastanum in winter condition showing terminal, axillary and adventitious buds. Axillary buds may be classified according to the number at a node into (1) alternate with a single bud at a node, (2) opposite, with two buds at a node on opposite sides of the stem, and (3) whorled with more than two buds at each node. Buds which arise anywhere on the plant except at the tips of stems or in the axis of leaves are called adventitious buds. In this figure, terminal bud is located at the tip. The leaf scars are left by the breaking away of the leaf stalks. Leaf trace scars are the broken ends of leaf traces. When the scales of terminal bud are shed a ring or girdle is left.

Pteridophytes (vascular cryptogams) : In the vascular cryptogams (lower tracheophyta) growth at the apex proceeds either from one or few initial cells, which are usually distinctive in their morphology (Bower, 1889; Hartel, 1838; Wardlaw, 1945). Most commonly the single apical cell is tetrahedral (pyramid like) in shape (e.g., in Psilotales, Equisetaceae, and ferns). The base of this pyramid is turned towards the free surface, and the new cells are formed at the

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other three sides. The Salvinia and Azolla (water ferns) have three sided apical cells with two sides from which new cells are cut off. In Selaginella apical growth occurs from a single three or four-sided apical cell or from a group of initials, and the two situations may be found in the same plant. The eusporangiate ferns have two or four initials, the leptosporangiate ferns have one, but there is no sharp line of division between the two groups with reference to this character. As regards their ontogeny much information supports the view that in the ferns the types of apex with several initials is more primitive that the zone with a single apical cell (Bower, 1890, 1935; Wardlaw, 1945).

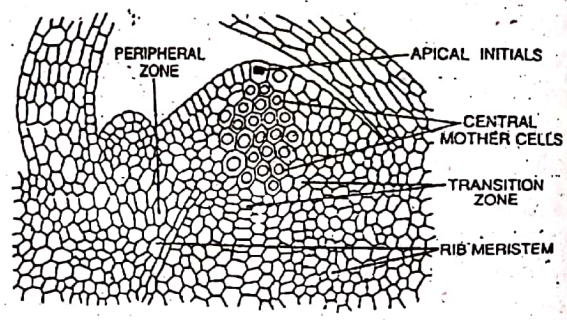

Fig. 19.4. The shoot apex. L. S. of shoot apex of Pinus strobus. Apical initials divide anticlinally contributing the cells to the surface layer, also divide periclinally adding the cells to central mother cell zone. The central mother cells divide actively and contribute to the transition zone. The products of these divisions form the rib meristem. (After K. Esau).

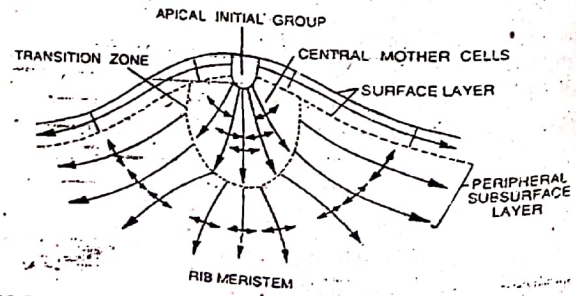

Fig. 19.5. The shoot apex. The zones and their mode of growth seen in the shoot apex of Ginkgo biloba in L. S. the apical initial group gives rise to the surface layer by anticlinal divisions, and adds to the central mother cells by periclinal divisions. The outermost products of divisions in the mother-cell zone are shifted toward the transition zone where they divide periclinally. (After Foster).

Gymnosperms : They commonly show several interrelated growth zones which are derived from a group of surface initials. These initials divide periclinally resulting in the formation of a subsurface group of cells, known as mother cells. The cell division is quite slow in the interior of this group but is active on its periphery. The derivatives of the divisions along the flanks of mothercell group combine with products resulting from anticlinal divisions of the apical initials. All together these lateral derivatives form a mantle-like peripheral zone of deeply stainable small cells which are less differentiated (eumeristem) than the mother cells and the cells or initiating zone. The derivatives produced at the base of the mother-cell zone become pith cells, and usually they pass through a rib-meristem form of growth. The art of the pith may arise from the peripheral zone. The peripheral mantle of cells, rich in cytoplasm, is the seat of origin of leaf primordia and of the epidermis, the cortex and the vascular tissues of the axis.

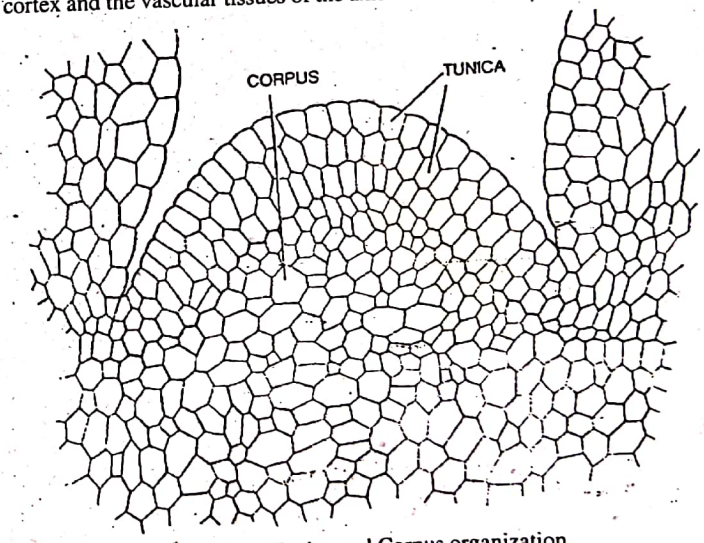

Fig. 19.6. Tunica and Corpus organization.

The details of above mentioned pattern vary in the different groups of gymnosperms. The cycads have wide apices and possess large number of cells in the initiating zone. This way the initiating zone occupies a large portion of the surface of the meristem and its periclinal derivatives converge towards the centre of the meristematic mound. This is characteristic of the cycads. The

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mother-cell zone in cycads is ill-defined. The rib meristem derived from the base of the central zone is conspicuous.

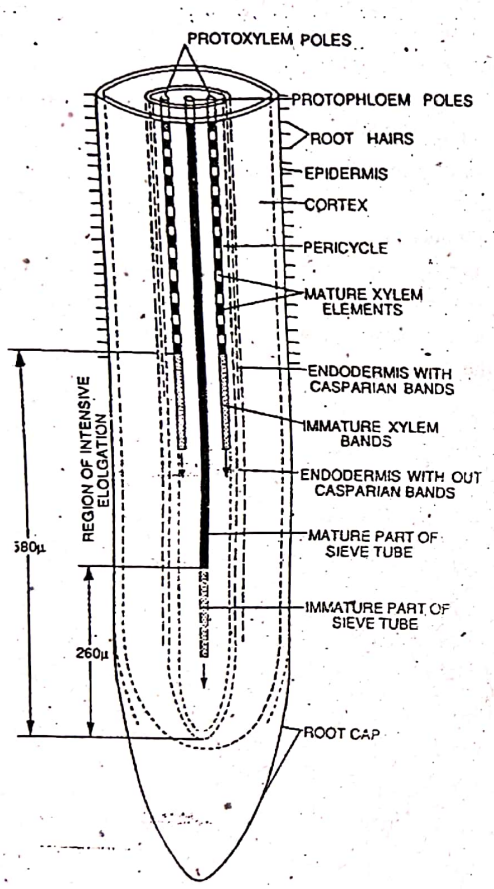

Fig. 19.7 L. S. of root tip of tobacco. The epidermis and the root cap show common origin. The cortex and the vascular cylinder have separate initials in the apical meristem. The pericycle is delimited close to the apical meristem. The sieve tubes mature first within the vascular cylinder. The root hairs develop beyond this region. The Casparian strips develop in the endodermis close to the position of first mature xylem elements. (After K. Esau.)

In Ginkgo the zones are quite conspicuous. The central mother-cell zone differentiates close to the apical initials. The rib meristem and the peripheral zones are sharply deliminated from the central zone.

The apical zonation in Pinus and other Coniferales is less diversified than in the cycads and less well defined than in Ginkgo.

In Gnetales, there is a definite separation into a surface layer and an inner core derived from its own initials. The shoot apices of Ephedra and Gnetum (Johnson, 1950) have been described as having a tunica-corpus pattern of growth.

Angiosperms : There is tunica-corpus organization in the shoot apex of angiosperms. One to five layered tunica have been observed in the dicotyledons, and one to three-layered in the monocotyledons. However, tunica-corpus organization is not found in Saccharum officinarum. To draw a clear cut demarcation line in between tunica and corpus is not simple matter. In angiosperms, the number of parallel periclinal layers in the shoot apex may vary during the ontogeny of the plant body and under the influence of seasonal growth changes.

In the angiosperms the segregation of apical-meristem zones is more definite than in lower groups. There are two sets of initials, one above the other, which give rise to tunica and corpus. The tunica has no or only rare periclinal divisions and ranges in thickness from several layers to one with two or three layers probably most frequent. The number of layers in the tunica may vary even in an individual plant.

Q. 20. *What is meristem ? Mention various types of meristem from position point of view.*

Ans. Tissue—A group of cells, which are alike in origin, structure, and funciton is called tissue. The plant body consists of *vegetative tissue* and *reproductive tissue.* In the higher plants the plant body is somewhat more complex in its cellular structure. The cells differ very much in their kind, form and origin in higher plants. The tissues may be groups into three principal groups. 1. *Meristems-or meristematic tissue.* 2. *Permanent tissue;* and 3. *Secretory tissue.*

Meristematic Tissues Or Meristems—In cellular plants, too much of growth takes place due to the new cell formation. A vascular plant, till it dies, produces new cells and forms new organs. In a young embryo all the cells can divide but as it matures into an adult plant, the new cells are formed only at the regions of the plant, body. These organized regions, concerned

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with growth are called meristem. The term meristem comes form Greek wo "meristems" means divisible, hence very active cell division takes pla meristematic tissues. Meristems are found only in plants, which occu throughout the life. The meristems are siutuated at the apices of root an shot.

The meristematic tissues show an absence of intercellular spaces. The cells are spherical or oval in shape. Each meristematic cell has cytoplas in abundance, a large nucleus and a thin wall, but vacuoles are not found but the initials of apicals meristems and cambium may have large siz vacuoles.

Classification of Meristems—Various systems of classifying meristem have been proposed by many eminent workers which are based on th characteristics such as, stage of development, position in plant body, origi function and topography. No system is exclusive and rigid. A few impor ta types have been discussed here.

1. Meristems Based on Stage Development

Promeristem or primordial meristem—Promeristem is the region o new growth in a plant body where the foundation of new organs or parts o organs is initiated. Sometiems it is also called *primordial meristem. Urmeriste and embryonic meristem.* From the viewpont of its structure this region consis of the initial and their immediate derivatives. The cells of this region ar isodiametric, thin-walled, vacuolate or non-vacuolate, with active cytoplas and erly stages of pis. Prominent nuclei and inconspicuous intercellular space amy be seen. As soon as the cells of this region begin to change in size, shap and character of wall and cytoplasm, setting off the beginning of tissu differentiatin, they are no longer a part of typical meristem; they have passe beyond that earlier stage.

Meristems based on origin of Initiating Cells

(i) Primary meristem : It is the first derivative of the promeristem and forms the fundamental parts of the plant. The chief primary meristems ar apices of roots and shoots and primordia of leaves and other similar appendages The cells of primary meristem divide in all possible planes.

The activity of primary meristems results in the built up of the primary body of the plant and in the growth in length of plant body. The dundamenta parts of the plant, its root, stem, branches and appendages originate from th primary meristms.

(ii) Secondary meristem : The meristems which appear after a certain stage of development of a plant organ are referred to as **secondary meristems.** These meristems develop from mature tissues which have already undergone differentiation. These are always lateral in position and are responsible for secondary growth in thichness. Such meristems develop either at the time of emergency (e.g., healing of wounds) or to effect secondary growth or to form cork.

3. Meristems based on position in the plant body

On the basis of their position in the plant body, meristems have been classified into the following three groups.

1. Apical Meristem—These are often called growing points and occur at he apex of stem or of the root. The growth in these meristem brings about increase in the length of the organs which organise to form the primary body of the plant. Growth begins by one or more apical initials which are situated at the tip of the organ. The apical initials maintain their individuality and position. Molitary apical cells occur in **Equisetales** and **Pteridophytes. In Spermatophytes,** group or groups of apical cells constitute the initiating body. The numebr of initials is usually constant for a given organ of a plant.

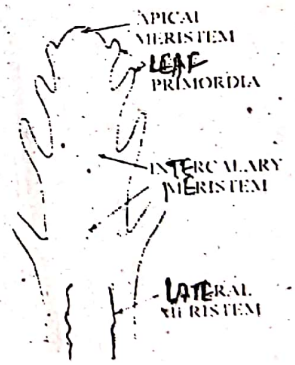

Fig. 20.1 : L.S. of Young stem showing different types of meristems.

2. Intercalary Meristems— Due to the growth of the apical meristem samll and large groups of active growing primary cells are left behind and become inserted between the perianent tissues. These are intercalary meristems. The common examples of this type of meristems are found in the basal portions

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of the internodes on *horsetails* and grasses and also at the basis of leavas in many plant. The growth of the leaves, flowers and fruits after their initiation is also regarded as due to the activity of intercalary meristems. Like the apical meristems. They are also responsible for the growth in length of the axis and the organs. These meristems function very slowly and therefore may persist for a long time chiefly in the stems but finaily transformed into permanent tissues.

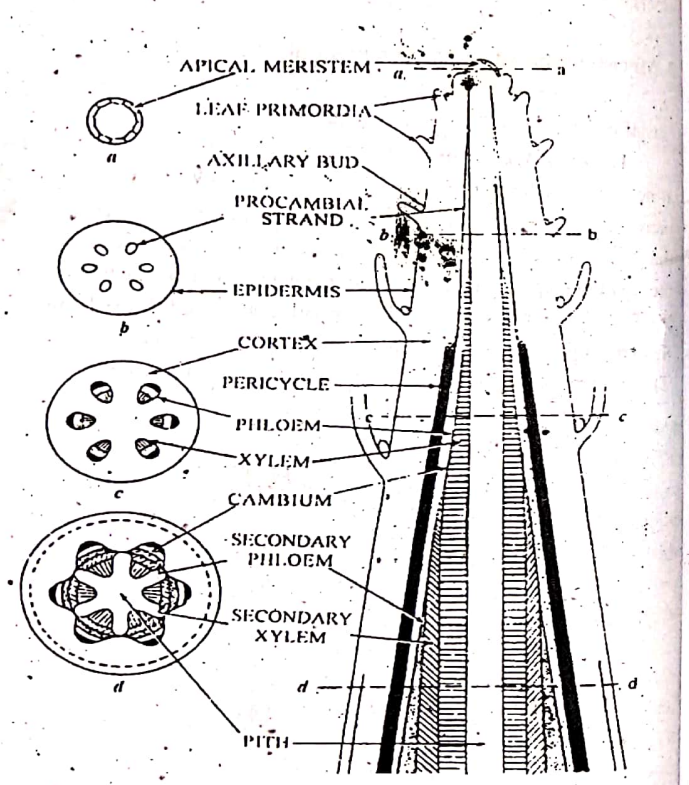

Fig. 20.2. : Stem apex showing Primary apical meristem and differentiation of tissues from cells formed by it.

3. Lateral Meristem—These are composed of initials that divide periclinally, the growth increases the diameter of the organ either by adding to the existing tissue or by forming new tissue. This process in often called the

secondary growth..Cambium and cork-cambium are the examples of the lateral meristem.

4. Meristems based on function :

According to **Haberlandt**, the primary meristem at tip of the root or stem apices have been groupes into the following three categories on the basis of their funcitons :

1. Protoderm—It develops the outermost layer called epidermis.

2. Frocambium—It develops into primary vascular tissues and form isolated strands of elongated cells outside the pith in the central region.

3. Ground meristem—It develops the cortes, pericycle, pith and medullary rays. This meristem is made up of large numebr of thin walled cells.

Q. 21. ***Describe the different theories of Apical Meristem.***

Ans. Shoot Apical Meristem : The shoot apex has been extensively studied by a number of workers and several theories have been put forward. **Gifford** (1954) has summarised these theories. The following theories have been proposed to explain the structural development and differentiation of the apical meristem.

1. Apical Cell Theory : It was proposed by **Hofmeister** (1857) and supported by **Nageli** (1878). According to this theory the primary meristem develops from a single apical cell e.g., **Crystogames**. Such a single apical cell occurs cell was also believed to the present in seed plants. The apical cell of the Pteridophytes is usually four-sided with three cutting faces but in some e.g. ***Salvia*** and ***Azolla***, it is three sided with two cutting faces.

2. Histogen Theory : It was proposed by **Hanstein** (1870). According to t his theory three distinct meristematic zones can be recognized in the shoot apex of angiosperms. These layers, each of which has its separate of initials, were termed as **histogens**. The outermost histogen was designated as **dermatogen**, the middle one as **periblem** and the innermost as **plerome**. Definite functions were assigned to each histogen. The dermatogen is destined to give rise to the epidermis, the periblem to the cortex and the plerome to the central cylinder. Subsequent studies revealed that the above layers have no morphological significance as they are not specific in their function. However, in most of the Gymnosperms and Angiosperms. It was not possible to distinguish these layers. Hence this theory which held ground for a long time was later dropped.

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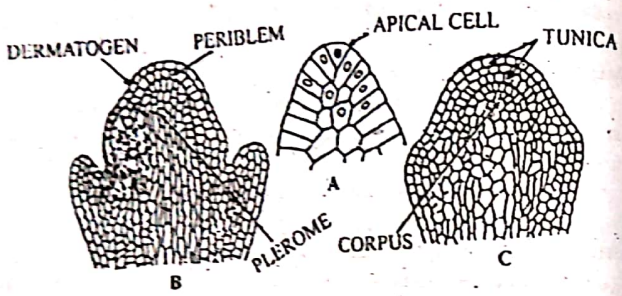


Fig. 21.1. Apical meristem (A) A single apical cell (B) Three histogen layers of Hanstein (C) Tunica and corpus of Schmidt.

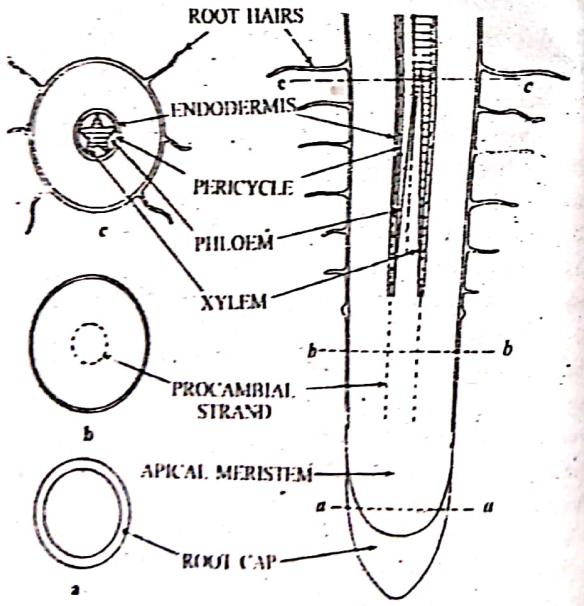
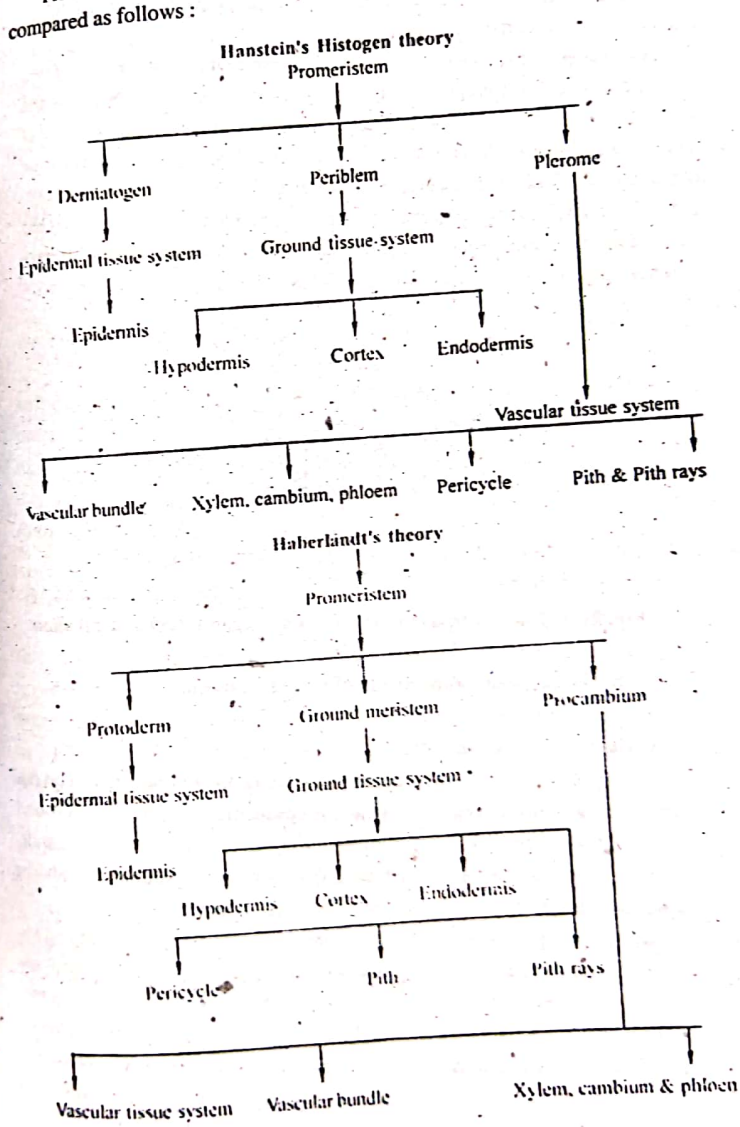


Fig. 21.2. Histogen theory : Position of dermatagen, pariblem and plerome on the shoot apex.

According to **Hanstein and Haberlindt** the meristematic tissues may be compared as follows :



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3. The Tunica Corpus Theory : This theory was propounded by **Schmid** *(1924)* and was developed a a result of increasing attention towards the devel*opment* and differentiation of shoot apex.

According to this concept the apical meristem of the stem consists of two more or less well differentiated regions : (1) The **Tunica** which forms the superficial layer and in which the cell divide mostly in an anticlinal manner and (2) the **Corpus** which forms the core of the shoot apex covered by the tunica and in which the cells divide in all planes. In the lower vascular plants, the differentiation between tunica and corpus is poor but in higher plants it has become quite distinct. In any case the tissues at the shoot apex can be differentiated into three more or less distinct regionis.

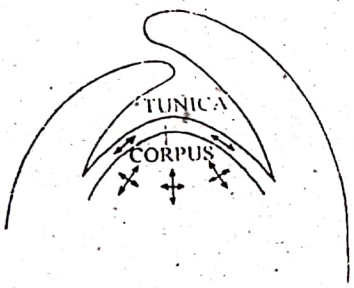

Fig. 21.3. Tunica corpus theory : showing organization of dicot shoot apex.

1. The promeristem or the region of the cell division.
2. The region of enlargment.
3. The region of maturation.

The region of cell enlargement lies just behind the promeristem. The derivatives of the **tunica** layer give rise to the **epidermis**. Groups of cell around the central core of cells elongated conspicuously and form procambial strands. In monocots the groups of cells which give rise to the procambial strands are scattered in the ground tissue enclosed by the epidermis.

In each group of procambial strand the inner cells develop spiral and annular thickenings and thus differentiate into the elements of protoxylem. Similarly a few elements of the procambial strands on the outer side develop into sieve-tubes and companion cells whch constitute the protophloem. However, the wall of procambial strands in between the protoxylem and protophloem is sti ll undifferentiated. Still later when the elongation of the procambial strands

(and also of the protoxylem elements) is complete the procambial elements just outer to the protoxylem develop scalariform, reticulate and pitted thickenings to form the metaxylem. Thus we see that the development of metaxylem is centrifugal leaving the protoxylem in the position. Inside the protophloem, more of the procambial elements form the sieve-tubes, companion cells and phloem parenchyma to form the primary phloem. In dicot stems, some procambial elements which have not yet given up their meristematic capacity remain as such and constitue the intrafascicular cambium is a left over of the apical meristem among the maturing tissues. The former, however, maintains its organic connection with the latter all through the length of the stem.

The drivatives of the **corpus** outer to the maturing procambial strands differentiate into the pericycle, endodermis and the cortex and those inner and latteral to them into the pith and the conjunctive tissue.

Primordia of young leaves arise just behind the promeristem by divisions in the derivatives of the tunica and the superficial layers of the corpus. Similarly the divisions in the tunica layer and the superficial layers of the corpus in the axil of leaves give rise to the primordia of axillary buds. Thus it would be seen that leaves and branches are exogenous in origin, in contrast at the lateral roots which arise by divisions in the pericycle and are thus endogenous in origin.

4. Histogenic Layer Theory

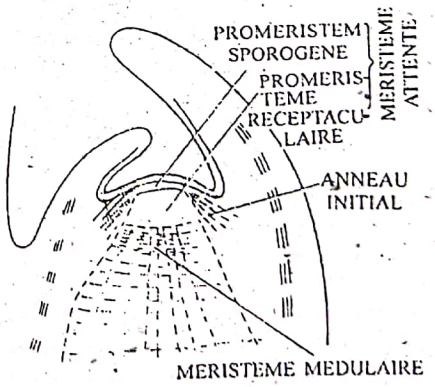

Fig. 21.4. Anneau initial and meristems d' attente theory showing the shoot apex of dicotyledon.

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Dermen (1947) induced Peach and Cranberry by colchicine treatment and suggested that tunica corpus may be replaced by **primary** histogenic layers in these cases. According to him in angiosperms there are three L-I, L-II and L-III basic **histogenic layers** which are found in various combinations of ploidy in the shoot apex. The cells of L-I and L-II may be 2X and L-III of 4X, which may form various combinations. From L-I layer, the epidermis o f stem & leaves are formed. The L-II layer forms 2-3 layered hypodermis or cortical tissues or in some cases a portion of vascular tissue. Usually L-III layer forms vascular tissue & pith. Therefore this th eory is regarded as the modification of **Hansteins** histogen theory.

5. Anneau Initial and Meristeme d' Attente Theory

This theory was given by **Buvat** (1955) which explains that during the vegetative phase of development, the peripheral and subterminal regions are actual initiating zones and the distal group of cells comparatively inactive which has no histogenic function. There are three apical meristems i.e., (i) **Anneau initial**—which is active peripheral zone, (ii) **Meristeme d'** attente—which is called waiting meristem and becomes active at the time of inflorescence formation and (iii) **Meristeme medullair**—which is called the central pith region.

According to this theory the centrally situated cells called waiting meristem were regarded as apical initials. **Ball** (1955), **Cutter** (1959) and **Loiseau** (1959) have explained that the waiting meristem divides actively and gives rise to a complete vegetative shoot.

6. Cyto-histological Zonation

In gymnosperms the shoot apices do not have surface layer which divides by anticlincal divisions. In *Ginkgo biloba*, according to **Foster** (1939) the shoot apex has certain zones of cytological characteristics, like.

(i) Apical initial group—It has a group of initials along the apical surface and their **lateral derivatives.**

(ii) Central mother cell Zone—This zone is found below the apical initial group and is formed by them. The cells of this zone have low rate of mitotic activity.

(iii) Rib meristem—It includes the centrally situated mother cells which form the pith.

(iv) Peripheral meristem—The cells of this zone are active & formed the leaf primordia and help in elongation of school.

According to **Popham** and **Chan** (1950) below the youngest leaf primordia a fifth zone is fund which is cup shaped & cealled the **cambium like zone.** This zone is found in *Bellis perennis, Chrysanthemium, morifolium* and *Ricinus communis*. This zone is formed during mid-plastochron and disappears as soon as plastochron comes to an end.

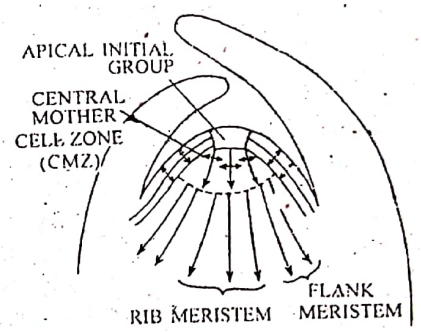

Fig. 21.6. Ginko bilobe : Shoot apex shaowing cyto histological zonation.

7. Regions of Shoot Apex

According to **Wardlaw** (1968) there are following five zones in the shoot apex.

(i) Distal region—It consists a group of initial cells which forms the meristem of the shoot.

(ii) Sub distal region—It forms the superficial layers of meristematic cells where growth takes place.

(iii) Organogenic region—Here the leaf initiation and tissue differentiation takes place.

(iv) Sub apical region—In this region cell division and cell elongation takes place and the internal tissues are differentiated.

(v) Maturation region—When tissue are mature there is no differentiation.

Many anatomists have reported that in the different zones of apical meristems different metabolites are distributed **Gifford** and **Corson** (1971) have found that in the soot apices of Acerpseudoplatanus, histochemical changes are formed due to the seasonal activities. It has been found the amount of R.N.A. is always high in spring and summer which gradually reduces in autumn and winter but there is an increase in lipids and starch. **Gifford** and **Tepper** (1962) worked on seedling apices of *Chenopodium ablum* found that R.N.A., D.N.A. histones and total proteins concentration in the central zone was less than in the cells of peripheral zone. These difference are less when the plant becomes old.

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Q. 22. *Explain about the Epidermal Tissue System.*

Ans. Epidermis. The epidermal tissue system is derived from the dermatogen of the apical meristem and forms the **epidermis** (*epi*, upon; *derma*, skin) or the outermost skin layer which extends over the entire surface of the plant body and is continuous except for certain openings (stomata and lenticels). At surface view the cells of the epidermis are somewhat irregular in outline (see Fig. 1), varying in shape and size, but closely fitted together without intercellular spaces. They, however, appear more or less rectangular in cross-section. Epidermis is mostly single-layered, but sometimes, as in the leaves of india-rubber plant, banyan, oleander, etc., it becomes few-layered, called *multiple epidermis*. Epidermal cells are parenchymatous in nature with comparatively small amount of cytoplasm lining the cell-wall and a alrge vacuole filled with colourless cell-sap. In some plants the cells may contain anthocyanins or chromoplasts, but not chlorplasts except in guard cells, ferns, submerged plants and a few others. In the leaves and young green shoots the epidermis, however, possesses numerous **stomata** through which an interchange of gases takes place between the plant and the atmosphere. Epidermal cells soon die off and become filled with various substances such as tannin, silica particles, gum, mucilage, crystals, etc. Inner and radial walls of epidermal cells are thin, while the outer walls are thick and usually impregnated with cutin or suberin. Cutinization or suberization sometimes extends to the radial walls also. The cutinized layer called the **cuticle** acts as a hard varnish-like coating and protects the inner cells against loss of water, mechanical injury and potential parasites (see below). Excretion of wax in the form of rods, scales, grains, etc., prevents further loss of water. In many plants epidermal cells often bear outgrowths, known as **hairs** or **trichomes**. These may be unicellular or multicellular, simple or branched, soft or sharp and stiff. Besides, the epidermis may also bear stinging hairs, as in nettles, glandular hairs, as in *Borehaavia* (B. PUNARNAVA; H. THIKRI), tobacco, *Plumbago* (B. CHITA; H. CHITRAK), etc. A dense coating of hairs, as in *Gnaphalium* and *Aerua*, is another feature of the epidermis.

The outermost layer of the root is called the **epiblema** or **piliferous layer**. It is mainly concerned with the absorption of water and mineral salts from the soil. Thus to increase the absorbing surface, which has been estimated to be 5 to 20 times greater, the outer walls of most of its cells extend outwards and form tubular unicellular prolongations called the **root-hairs**. The epiblema is neither cutinized nor is it provided with stomata.

Functions : (1) The primary function of the epiderms is the protection of the internal tissues against mechanical injury, excessive heat or cold, fluctuations of temperature, attack of parasitic fungi and bacteria and against leaching effect of rain; this is due to the presence of cuticle, hairs, tannin, gum, etc. (2) Prevention of excessive evaporation of water from the internal tissues by the development of thick cuticle, wax and other deposition, cutinized hairs, scales, multiple epidermis, etc., is another important function of the epidermis. (3) Protection of the plant against intense illumination (i.e., strong sunlight) and against excessive radiation of heat is mainly afforded by strong cuticle and cutinized hairs, particularly a dense coating of hairs. (4) The epidermis has also to protect the plant against the attack of herbivorous animals; this the epidermis does with the help of sharp and stiff hairs as in some cucurbits, a dense coating of hairs as in *Gnophalium*, stinging hairs as in nettles silica particles as in many grasses (lemon grass, for example), *Equisetum*, etc., and raphides as in many aroids. (5) The epidermis also acts as a store-house of water, as in desert plants. (6) The epidermis sometimes has some minor functions such as photosynthesis, secretion, etc.

Stomata. *Structure and Behaviour.* Stomata (*stoma*, a mouth) are very minute openings (Fig. 1) formed in the epidermal layer in green aerial parts of the plant, particularly the leaves. Roots and non-green parts of the stem are free from them. Each stoma is surrounded by two semi-lumar cells, known as the *guard cells*. The term 'stoma' is often applied to the stomatal opening plus the guard cells. The guard cells are living and always contain chloroplasts, and their inner walls are thicker and outer walls thinner. They guard the stoma or the passage, i.e., they regulate the opening and closing of it like lips. Sometimes the guard cells are surrounded by two or more cells which are distinct from the epidermal cells; such cells are called *accessory cells*. In dicotyledonous leaves the stomata remain scattered, while in monocotyledonous leaves they occur in parallel rows. Under normal conditions the stomata remain closed at night, i.e., in the abdsence of light and they remain open during the daytime, i.e., in the presence of light. In most plants the stomata open fully only in bright light, but in certain plants the stomata open fully only in bright light, but in certain plants the stomata do so in diffuse light. Commonly they open fully in the morning and close towards the evening. They may close up ato daytime when very active transpiration (evaporation of water) takes place from the surface of the leaf under certain conditions such as dryness of the air, blowing of dry wind and deficient supply of water in the soil. The intensity of light

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markedly affects the degree of stomatal opening. The opening and closing of the stomata are due to the movement of the guard cells. When the guard cells become turgid, i.e., full of water, they expand and bulge out in the outward direction, and the stoma is open; when the guard cells become flaccid by losing water the stoma is closed.

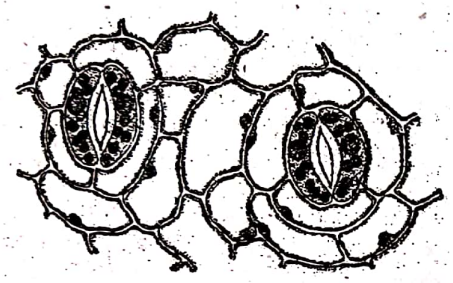

Fig. 22.1. Stomata (surface view in epidermal layer.)

The turgidity or flaccidity of the guard cells is due to the presence of sugar or of starch in them. In light the sugar manufactured by the chloroplast of the guard cells accumulates in them and, being soluble, increases the concentration of the cell-sap. Under this condition the guard cells absorb water from the neighbouring cells and become turgid, and the stoma opens. In darkness on the other hand the sugar present in the guard cells becomes converted into starch—an insoluble compound. The concentration of the cell-sap is, therefore, lower than that of the neighbouring cells. Under this condition the guard cells lose water and shrink and the stoma closes. The transformationof sugar into starch at night and vice versa at daytime is due to acidity and alkalinity of the cell-sap of the guard cells. At night hypothosynthesis being in abeyance carbon dioxide accumulates in the guard cells and the cell contents become weakly acid. Under this condition sugar becomes converted into starch. During the daytime carbon dioxide is utilized in photosynthesis and thus the cell contents become slightly alkaline. Under this condition the starch becomes converted into sugar.

There is another hypothesis, called **colloidal hypothesis**, put forward to explain the movement of the guard cells. According to this, the cell contents become alkaline as a result of the effect of sunlight on guard cells and this causes the colloids present in them to swell, apart from the fact that this causes the transformation of starch into sugar. The swelling of the colloids according

to this theory causes the guard cells to bulge out and the stoma to open. At night the acidity of the guard cells increases and causes the colloids to shrink again, and thus to close the stoma, apart from the fact that this increased acidity brings about the conversion of sugar into starch.

Functions and Distribution. Stomata are used for interchange of gases between the plant and the atmosphere—poxygen for rspiration and carbon dioxide for manufacture of carbohydrates. For the facility of diffusion of these

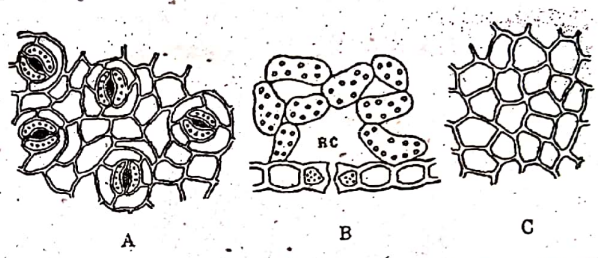

Fig. 22.2. Stomata in betel leaf. A. lower epidermis with numerous stomata (surface view), B. section of leaf (a portion of the lower side) : RC, repiratory cavity internal to a stoma: C. upper epidermis with no stoma (surface view).

gases each stoma opens internally into a small, cavity, known as the *respiratory cavity* (Fig. 22.2 B) which in its turn communicates with the system of intercellular spaces and air-cavities. Stomata are also the organsthrough which evaporation of wawter normally takes place and the plant thus gets rid of the excess quantity. Stomata are most abundant in the lower epidermis (Fig. 22.2) of the dorsiventral leaf; none or sometimes comparatively few) are present in the upper (Fig. 22.1), e.g., in sunflower leaf the average numbers in lower and upper surfaces are 325 and 175, in pea leaf 216 and 101, in gourd leaf 269 and 28, etc. In the isobilateral and centric leaves stomata are more or less evenly distributed on all sides. In the floating leaves, as in those of the water lily, stomata remain confined to the upper epidermis alone; in the submerged leaves no stoma is present. In desert plants and in those showing xerophytic adaptations, e.g., American aloe or century plant (*Agave;* Fig. 22.3), oleander (*Nerium*; Fig. 22.4), pine (*Pinus*; see Fig. VI/10), etc. one or more stomata are situated in grooves or pits in the leaf. This is a special adaptation to reduce excessive evaporation, as the stomata sunken in pits are protected from gusts of wind. The number of stomata per unit area varies within wide limits. In ordinary land

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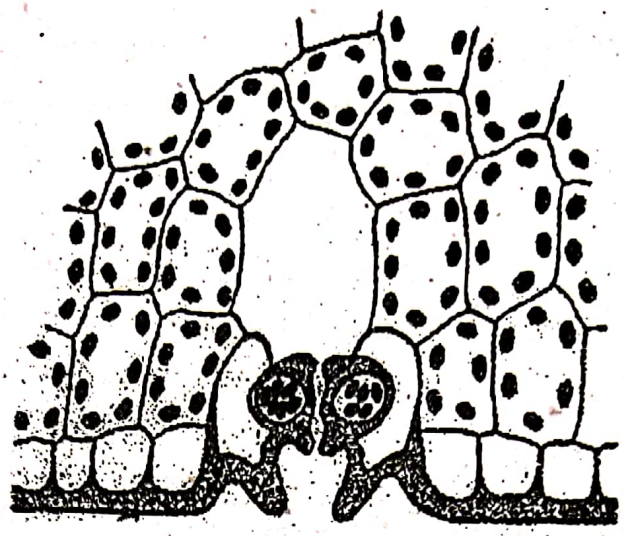

Fig. 22.3. Sunken stoma in the leaf of American aloe (Agave).

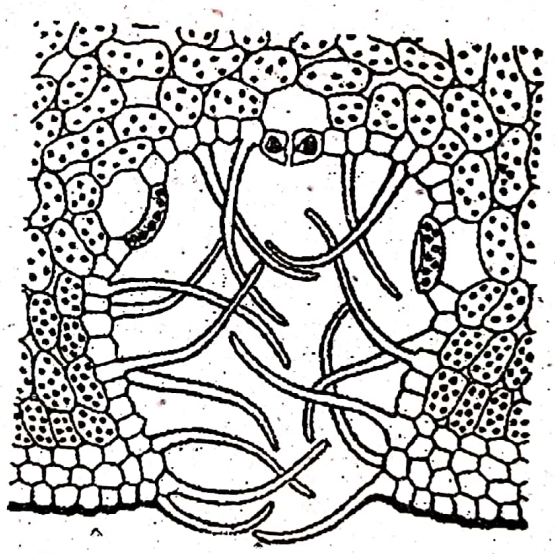

Fig. 22.4. Sunken stomata stomata in the leaf of oleander (Nerium).

plants there is an average of about 100 to 300 stomata per square millimetre, sometimes much less or many more. In the floating leaveds of aquatic plants stomata may be as many as 400 per square millimetre, while in submerged leaves there are none. In desert per square millimeter; while there are cases with about 1,300 stomata in the same space.

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